

FEEDING MECHANISMS AND THE FORCES INVOLVED IN SOME BLOOD-SUCKING INSECTS

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In the stages of *Cimex lectularius* L. and *Pediculus humanus* L. and in adult female *Aedes aegypti*(L.) the weight of the blood meal was greater than the body weight. In *C. lectularius* L. and *P. humanus* L. the negative pressure required to draw the blood to the cibarial pump decreased from the first to the second instar and then increases to a maximum in the adult. This pressure may be as high as 5.6×10^5 dyne/cm². In *A. aegypti* female it is smaller than any instar of *C. lectularius* or *P. humanus*. The muscular tension of the cibarial pump dilators in the species studied ranged from 5.7 to 18.4×10^3 g/cm² and the power output ranged from 2.75 to 13.3×10^3 g cm/sec/g of muscle. Sensilla were found in the cibarium of *C. lectularius* but not of *P. humanus*.

Blood-sucking insects can ingest enormous meals in a short time. In view of the narrowness of the feeding canal and viscosity of vertebrate blood, the rate of feeding, the negative pressure produced in the cibarial pump, and the power required from the cibarial pump dilators are of interest. All the nymphal instars and the adult males and females of *Cimex lectularius* L. and *Pediculus humanus* L., as well as adult females of *Aedes aegypti* (L.) were studied.

The structure and many details in the mechanism of sucking apparatus in Hemiptera have been studied by Weber (1928, 1928a, 1929), Dickerson and Lavoipierre (1959), and Lavoipierre et al. (1959). Kemper (1932) and Snodgrass (1935, 1944) described in detail the feeding apparatus in the bedbug *C. lectularius*.

The anatomy of the mouth parts of some mosquitoes has been described in detail by Vogel (1924), Robinson (1939), Gordon and Lumsden (1939), Christophers (1960), Schiemenz (1957), and Clements (1963). The weight of the blood ingested by the females of different species of mosquitoes and the rates of the ingestion have been reported in many publications. Fulleborn (1908) reported the blood taken by gorged *A. aegypti* averaged 0.75 mg with a minimum and maximum of 0.20 and 0.84 mg respectively. He also found that 53 out of 137 took a blood meal much greater than their own weight. Jeffery (1956) recorded that *Anopheles quadrimaculatus* and *Anopheles albimanus* ingest about 3.46 and 2.58 mg of blood respectively. Christophers (1960) reported that the feeding canal in *Aedes aegypti* is about 2 mm long and has a diameter of 0.03 mm. He added that from 2 to 4 mm³ of blood pass through this channel in 2 minutes and that the linear rate of flow is from 2 to 4 cm/sec.

The morphology of the piercing organs in Siphunculata has been dealt with by Cholodkowsky (1904), Enderlein (1905, 1905a), Pawlowsky (1906), Harrison (1914), Sikora (1916), Peacock (1918), Florence (1921), Vogel (1924), Fernando (1933), Snodgrass (1944) and Stojanovich (1945). Summarized accounts are also given by Patton and Evans (1929), Metcalf and Flint (1962), and Imms (1960). The relationships between food supply and the biology of *Pediculus humanus* have been described by Nuttall (1917), Buxton (1947), Busvine (1948) and Gooding (1963).

Feeding Apparatus and Feeding Mechanisms

Whole mounts of the head and mouthparts were prepared. The insects were soaked overnight in 5% potassium hydroxide solution, washed thoroughly in water, stained with acid fuchsin if necessary, dehydrated in ethanol, cleared in xylol and mounted in canada balsam. Serial cross sections of the mouthparts and the head, and serial horizontal sections of the head were necessary. Mallory's triple stain was used. Measurements were made with an ocular micrometer.

The mouthparts of the bedbug *C. lectularius* (fig. 4) consist of a labium considerably longer than the head and when not in use turned backwards at its base with its distal part between the forelegs. The labium is four-segmented with the first one mostly concealed by the labrum and the maxillary lobes. The labium is grooved on the lower surface and the sides diverge near the tip of the last segment to leave a small aperture. The maxillae and the mandibles are stylet-like and are held together within the groove of the labium. Between the maxillary stylets is a minute salivary duct and a relatively large food canal. The length of the food canal and its radius vary from one instar to the next (table 2). At the base of the labium the maxillae turn backwards into the head pouches and diverge against the base of the hypopharynx where the food canal opens into the anterior surface of the hypopharyngeal lobe that leads back into the cibarial pump. The hypopharynx is a small lobe and its dorsal surface is continued back into a large and deeply concave sitophore with strong lateral margins, which is the floor of the cibarial pump (fig. 2). The dorsal wall of the cibarial pump is in the form of a diaphragm (d.) which is attached by a rubbery margin (r.m.) along either edge of the sitophore (sit.). The diaphragm when not in action is completely collapsed into the cavity of the sitophore. The measurements of the various parts of the cibarial pump in the different instars are shown in tables 3 and 4. The dilator muscles (m.) consist of two lateral bundles of fibers, arising on nearly the whole clypeus. Measurements of these muscles are shown in tables 3 and 4. The cibarial pump discharges directly into the tubular oesophagus as there is no differentiated pharynx.

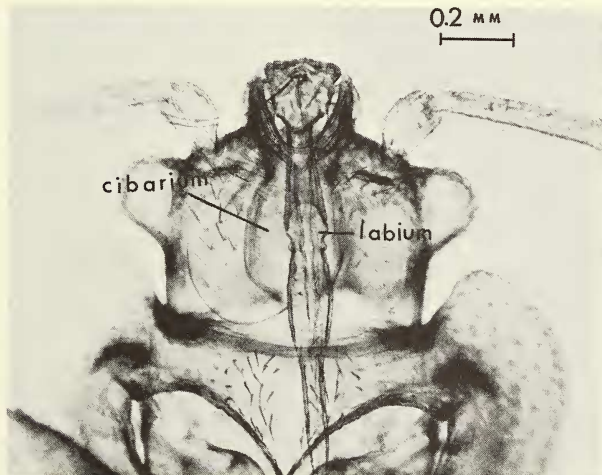


Fig. 1. Head and mouthparts of female *C. lectularius* (ventral view).

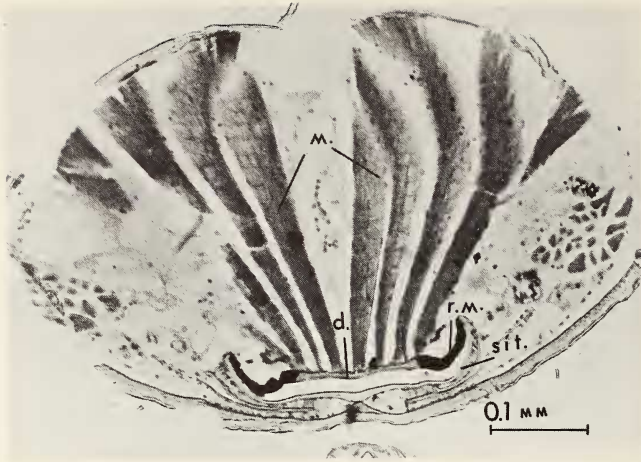


Fig. 2. Cross section through the head of female *C. lectularius*. (d) diaphragm; (rm) rubbery margin; (m) cibarial pump dilators.

When the bedbug feeds the stylets are forced into the skin of the host. The labium helps in lowering the head of the insect near the skin of the host by a backward bending of the third and fourth segments. The mandibular stylets are the effective piercing organs while the two maxillary stylets closely adhere to act as a sucking needle. Contraction of the cibarial pump dilators moves the diaphragm upwards during the filling stroke. Emptying is achieved by the return of the diaphragm under the elastic force of the rubbery margins.

The mouthparts of female *A. aegypti*, like those of *C. lectularius*, are modified for piercing and most of the mouthparts are extended into long and slender stylets. The labium is relatively stout and contains a dorsal groove in which the stylets lie closely beside each other in a fascicle. The labium ends with a pair of labella. The labrum is a broad pointed stylet in the labial groove. It is curved so that its edges meet and thus forms the food canal. Towards the base of the labrum the edges separate and the hypopharynx forms the floor of the food canal. The average length and the radius of the food canal are shown in table 2. The hypopharynx is a very slender stylet with a median rib containing the salivary canal. The mandibles are also stylets which come to a simple point without teeth at the tip. The maxillae, which are the principal piercing organs, each consist of a long flattened stylet with a curved end. The cibarial pump (cb.), fig. 3, is located under the clypeus (cl.) and is trough-shaped. The lower wall of the trough is well-sclerotized and is continuous with the upper surface of the hypopharynx. The upper wall is thinner and is continuous with the inner surface of the labrum. The upper wall is elastic and when the cibarial pump is not in action it lies close to the lower wall. Attached to the upper wall of the cibarial pump are two bundles of muscles, the dilators of the cibarial pump (m.), which have their

origin from the clypeus. Measurements of the cibarial pump and its dilators are shown in tables 3 and 4. For a short distance behind the cibarial pump the cuticle is thin and forms a valve. The cibarial pump is connected to the pharyngeal pump by a narrow canal.

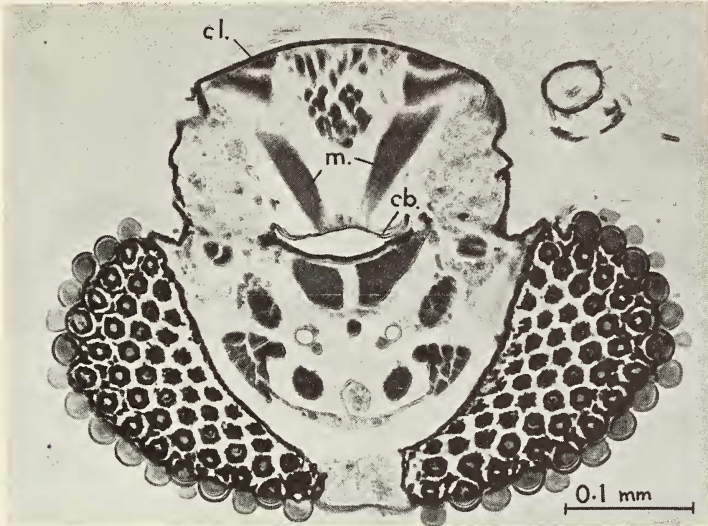


Fig. 3. Cross section through the head of female *A. aegypti*. (cb) cibarial pump; (cl) clypeus; (m) cibarial pump dilators.

The head of *P. humanus* is produced anteriorly into a very small snout-like proboscis probably formed from the labrum and in which is a terminal opening or prestomum. This snout-like proboscis is armed internally with small teeth used to grip the host during feeding. The prestomum opens to a preoral cavity within the head, the upper part of it is continuous with the cibarial pump; the lower part extends to a long sac which contains the stylets and nearly reaches the posterior end of the head. The three stylets lie one above the other, the dorsal and ventral ones forked at their bases. The dorsal stylet is made of two united halves with the edges curved upwards and rolled over each other to form the food canal. The ventral stylet is the effective piercing organ and its apex is armed with teeth. The median stylet is pierced throughout its length by the salivary duct. The homology of these stylets with the mouthparts of biting insects has been a subject of dispute for many years. Scholzel (1937) reinvestigated the development of these mouthparts. He claimed that the ventral stylet is the labium, and he said that the maxillae and mandibles are reduced and merged into the lateral walls of the preoral cavity and that the dorsal and median stylets are both derived from the embryonic hypopharynx. This interpretation was accepted by Snodgrass (1944). During feeding the blood passes through the food canal of the dorsal stylet into a trough that fits into the proximal end of the food canal. This trough, which is closed dorsally by the inner clypeal wall, is connected with the cibarial pump. Fig. 4 shows the action of the cibarial pump during the filling and emptying strokes. The mea-

surements of the feeding canal and the various parts of the cibarial pump are shown in tables 3 and 4.



Fig. 4. Cross section through the head of the female *P. humanus*. A. During filling stroke. B. During emptying stroke. (cb) cibarial pump; (m) cibarial pump dilators.

Sense Organs in the Food Canal

Von Gernet and Buerger (1966) studied the labral and cibarial sense organs in some mosquitoes. They suggested that food is detected by the apical labral sense organs and the pumping action is initiated by impulses received by the cibarial muscles from the labral sense organs via the frontal ganglion. They also suggested that the cibarial sense organs control the openings of the stomach and diverticula, thus setting the food-directing mechanism in action.

Similarly, I studied *C. lectularius* and *P. humanus*. No sense organs

could be located on the maxillae of *C. lectularius*. On the other hand, two types of sensilla were found in the cibarium. A dorsal group consists of six sensilla at the anterior end, three on each side of the cibarium (fig. 5A). These are formed from minute hollow spines and innervated by fine dendrites originating from the adjoining sensory cells. These sensory cells seem to be innervated by a branch from the frontal nerve. The second group consists of two campaniform sensilla, one on each side of the sitophore (fig. 4B). Miles (1958) found that *Oncopeltus* and *Dindymus versicolor*, could discriminate between liquids sucked up the feeding canal while any contact receptors were masked.

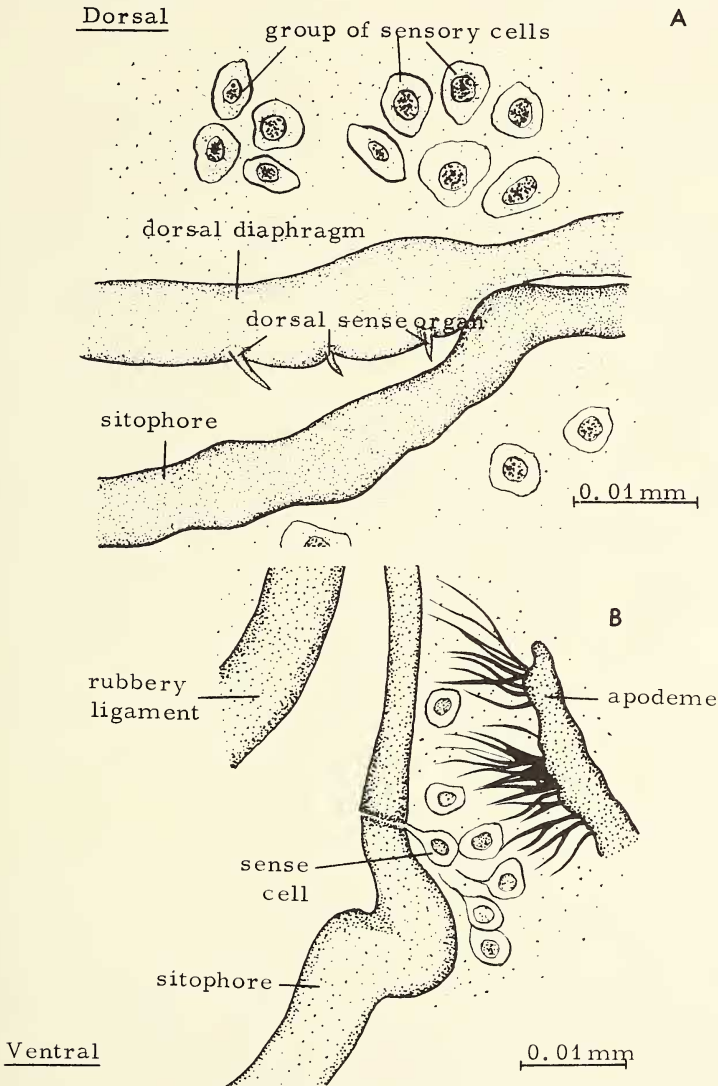


Fig. 5. Sense organs in the cibarium of female *C. lectularius*. A. Dorsal sense organs. B. Sitophore sense organs.

No sensory organs could be located in the food pathway of *P. humanus*.

Rate of Feeding and the Forces Involved

Methods

Feeding was observed under a binocular microscope and the feeding period was timed with a stop watch. The weight of the blood meal was determined by weighing the insects on a torsion balance before and after feeding. In all the experiments the insects were fed naturally on human blood.

Calculation of the pressure difference required to force a liquid along a tube at known rate can be made from Poiseuille's formula:

$$\Delta P = \frac{8 Q \eta}{\pi r^4 t}$$

where ΔP = pressure difference in dynes/cm²

Q = volume moved in cm³, η = viscosity of the liquid in poises, l = length of the tube in cm, r = radius of the tube in cm, t = time in seconds.

Poiseuille's formula was applied for the determination of the negative pressure required to draw the blood to the cibarial pump in these insects, on the assumption that the blood behaves like a simple fluid and the flow is laminar, because no more precise procedure has been developed. These assumptions are questionable.

The volume of the blood (Q cm³) ingested during feeding for t seconds was determined from the weight, taking the density of human blood as 1.056 g/cm³ (Spector 1956, p. 51). The viscosity of human blood is approximately 0.025 poises at 38 C (Mitchell 1948, p. 407). The negative pressure in the cibarium was obtained by subtracting from the pressure difference the capillary blood pressure which is 12 mm Hg or 1.6×10^4 dynes/cm² (Wright 1952). The muscular force required to provide this negative pressure was calculated by multiplying the corrected pressure difference by the area of the diaphragm.

The force obtained from these calculations was doubled for the estimation of the tension of the cibarial pump dilators on the assumption that half of the time is spent in the filling stroke. The muscular tension per unit cross sectional area of muscles was obtained by dividing the corrected force by the mean cross sectional area of the cibarial pump dilators. The mean cross sectional area was determined from cross sections of the cibarial pump dilators cut at 6 microns.

The power required of the cibarial pump dilators expressed as ergs/sec/g of muscle was found by multiplying the force by the total working travel of the diaphragm in a second and dividing by the weight of the cibarial pump dilators. The total working travel was determined by multiplying the width of the rubbery margin (length in section, fig. 2) by the number of pump cycles per second. The geometry of the cibarium, flat and expanded, suggests that the diaphragm moves a distance approximately equal to the width of the rubbery margin in each stroke. For determining the weight of these muscles the volume was obtained by multiplying the mean cross sectional area by the length of muscles and assuming the specific gravity of insect muscle to be one.

The rates of feeding observed are shown in table 1.

TABLE 1. Feeding period, weight of blood meal, and rate of feeding in *C. lectularius*, *P. humanus*, and *A. aegypti* females.

Species & stage	Time to engorgement in seconds	Weight of meal (mg)	Wt <u>meal</u> / body	Blood taken per sec (μ g)	Pump cycles/ second	Blood taken/pump cycles (μ g)
<i>C. lectularius</i>						
First	146.5 \pm 17.4* (20)	0.26 \pm 0.06* (20)	3.7	1.77 \pm 0.045* (20)	4.0 \pm 0.05* (40)	0.44
	105 - 187	0.13 - 0.44		1.23 - 2.35	2.9 - 4.6	
Second	156.8 \pm 4.2 (20)	0.62 \pm 0.06 (20)	4.5	3.95 \pm 0.15 (20)	3.8 \pm 0.04 (36)	1.03
	129 - 190	0.22 - 0.92		1.63 - 4.84	3.2 - 4.5	
Third	175.3 \pm 4.3 (25)	1.09 \pm 0.09 (25)	3.2	6.20 \pm 0.13 (25)	3.3 \pm 0.04 (28)	1.89
	135 - 282	0.46 - 1.82		3.41 - 6.62	3.0 - 3.8	
Fourth	234.4 \pm 8.8 (20)	2.86 \pm 0.09 (25)	4.4	11.73 \pm 0.14 (25)	3.3 \pm 0.02 (40)	3.58
	135 - 282	1.14 - 3.01		8.44 - 12.04	2.9 - 3.6	
Fifth ♀	305.6 \pm 4.1 (15)	5.64 \pm 0.35 (20)	4.9	18.46 \pm 0.48 (25)	3.0 \pm 0.03 (20)	6.18
	240 - 422	2.21 - 8.42		9.21 - 19.98	2.7 - 3.3	
Fifth ♂	290.0 \pm 5.9 (15)	5.42 \pm 0.31 (15)	4.8	18.69 \pm 0.76 (15)	3.0 \pm 0.03 (20)	6.29
	240 - 310	2.64 - 8.10		11.00 - 26.2	2.8 - 3.3	
Adult ♀	268.9 \pm 10.3 (19)	6.48 \pm 0.41 (15)	2.8	24.10 \pm 0.72 (15)	2.4 \pm 0.02 (30)	9.88
	213 - 350	5.20 - 11.20		19.24 - 32.0	2.3 - 2.5	
Adult ♂	286.9 \pm 14.6 (20)	6.23 \pm 0.41 (15)	2.8	21.70 \pm 0.46 (15)	2.4 \pm 0.02 (30)	8.89
	195 - 410	3.90 - 11.4		20.86 - 27.91	2.3 - 2.5	

TABLE 1 (cont.).

Species & stage	Time to engorgement in seconds	Weight of meal (mg)	Wt meal/body	Blood taken per sec (μ g)	Pump cycles/second	Blood taken/pump cycles (μ g)
<i>P. humanus</i> **						
First	504.0 \pm 7.7 (15)	0.11 \pm 0.005 (15)	1.8	0.22 \pm 0.006 (15)	2.8 \pm 0.23 (15)	0.08
	445 - 565	0.08 - 0.13		0.18 - 0.25	2.1 - 3.3	
Second	443.1 \pm 9.2 (15)	0.21 \pm 0.007 (15)	1.4	0.48 \pm 0.008 (15)	5.3 \pm 0.03 (21)	0.09
	275 - 720	0.15 - 0.30		0.40 - 0.53	5.0 - 5.6	
Adult ♀	764.4 \pm 45.6 (20)	1.13 \pm 0.078 (18)	1.2	1.48 \pm 0.027 (15)	4.6 \pm 0.001 (38)	0.32
	459 - 1372	0.82 - 1.80		1.34 - 1.80	3.9 - 5.0	
Adult ♂	782.9 \pm 48.4 (15)	0.95 \pm 0.07 (15)	1.1	1.21 \pm 0.016 (15)	4.2 \pm 0.06 (15)	0.29
	430 - 1210	0.50 - 1.40		1.14 - 1.31	3.7 - 4.5	
<i>A. aegypti</i>						
Adult ♀	255.1 \pm 8.8 (15)	1.62 \pm 0.18 (15)	1.2	6.35 \pm 0.34 (15)	4.9 \pm 0.20 (15)	1.29
	210 - 295	0.84 - 2.90		4.00 - 9.83	4 - 6	

* Mean \pm SE
(number of insects used)
Range

** Third nymphal instar of *P. humanus* was not studied because of some difficulties in maintaining the culture.

Rate of Feeding

The feeding period of *C. lectularius* and *A. aegypti* females was taken as the time required for the insect to feed till engorged and of *P. humanus* as the time required for the insect to feed till the blood started to exude from the anus.

The feeding period of *C. lectularius* is a minimum in the first nymphal instar, increases to a maximum in the fifth instar and then decreases in the adult. The feeding period of the adult female is shorter than that of the male.

In *P. humanus* the feeding period of the first instar is slightly longer than that of the second instar and shorter than that of the adult. The feeding period of the female is shorter than that of the male. The feeding period in *P. humanus* is much longer than in *C. lectularius* and in *A. aegypti* female, that to engorgement would be longer still. The duration of the

feeding period can be correlated with the behaviour of these insects and their access to their hosts. The longer feeding period in *P. humanus* may be related to their living on the host while both *C. lectularius* and *A. aegypti* leave their host after feeding.

The feeding period of the female *A. aegypti* is longer than that of each one of the first four instars and shorter than that of the fifth instar and the adult of *C. lectularius*.

When the insects feed till engorgement the weight of the blood meal varies from one instar to the next. In *C. lectularius* and *P. humanus* the minimum value is found in the first nymphal instar and the maximum in the adult stage. The weight of the female's blood meal was greater than the male's in both *C. lectularius* and *P. humanus*. The weight of the blood meal in *C. lectularius* is greater than that in *P. humanus*. The weight of the blood meal in *A. aegypti* is greater than that of any instar in *P. humanus* and that of the first three instars of *C. lectularius*, but smaller than that of the other instars in the latter species.

In all three species the weight of the blood meal is greater than the body weight. The ratio of weight of the blood meal to body weight is greater in *C. lectularius* than in the other two species. In *C. lectularius* and *P. humanus* the ratio is higher in the nymphal instars than in either the female or the male because of the flexibility of the integument which becomes more sclerotized in the adult stage. In *C. lectularius* the number of pump cycles per second decreases gradually from the first instar to the adult stage. In *P. humanus* the number of pump cycles per second increases from the first to the second instar and then decreases slightly in the adult stage.

The rate of feeding in *C. lectularius* and *P. humanus*, expressed as micrograms of blood taken per second or as micrograms of blood taken per pump cycle, increases gradually from the first instar to the adult. The rate of feeding is greater in the adult female than in the male in both species. In the first nymphal instar of *C. lectularius* the rate of feeding is much greater than in any instar of *P. humanus*. The weight of blood taken per second by *A. aegypti* females is greater than that taken by the first three nymphal instars of *C. lectularius* and smaller than that taken by each of the other instars. On the other hand, the weight of blood taken per pump cycle in *A. aegypti* is greater than in the first and second instars of *C. lectularius* and smaller than in the other instars.

Negative Pressure in the Cibarial Pump

Table 2 shows the negative pressure required to draw the blood to the cibarial pump at the observed rates in these insects. In *C. lectularius* the pressure difference decreases from the first to the second nymphal instar and increases from the second to the adult stage. The pressure difference in female *A. aegypti* is smaller than in any instar of *C. lectularius* and than in the first instar and the adult stage of *P. humanus*. In the last species it decreases from the first to the second nymphal instar with a maximum value in the adult. Table 2 also shows the results obtained by Bennet-Clark (1963) for the fifth nymphal instar of *Rhodnius prolixus* (Stahl). He claimed that 1.96×10^6 dynes/cm² or about 2 atmospheres, can be taken as the likely minimum, but he ignored the proximal 5 mm of the feeding canal and assumed that the viscosity of the blood is equal to that

of water. He added that if he took these into consideration the pressure required for *Rhodnius* to feed could be as high as 9 atmospheres, i.e. 9.12×10^6 dynes/cm².

TABLE 2. Negative pressure (relative to atmospheric) in the cibarial pump in *C. lectularius*, female *A. aegypti*, *P. humanus* and *R. prolixus*

Species & stage	Q/t cm ³ /sec	l* = length cm	r* = mean radius cm	▲ P dyne /cm ²	▲ P** corrected dyne/cm ²
<i>C. lectularius</i>					
First	1.7x10 ⁻⁶	0.055 (20) 0.050-0.058	4.4x10 ⁻⁴ (5) 4.1x10 ⁻⁴ -4.9x10 ⁻⁴	1.6x10 ⁵	1.4x10 ⁵
Second	3.7x10 ⁻⁶	0.064 (15) 0.060-0.069	6.0x10 ⁻⁴ (7) 5.8x10 ⁻⁴ -6.4x10 ⁻⁴	1.1x10 ⁵	9.4x10 ⁴
Third	5.9x10 ⁻⁶	0.079 (15) 0.073-0.082	6.6x10 ⁻⁴ (5) 6.5x10 ⁻⁴ -6.8x10 ⁻⁴	1.6x10 ⁵	1.4x10 ⁵
Fourth	1.1x10 ⁻⁵	0.097 (15) 0.090-0.102	6.8x10 ⁻⁴ (5) 6.7x10 ⁻⁴ -6.9x10 ⁻⁴	3.3x10 ⁵	3.1x10 ⁵
Fifth	1.8x10 ⁻⁵	0.097 (15) 0.094-0.109	7.0x10 ⁻⁴ (5) 6.8x10 ⁻⁴ -7.2x10 ⁻⁴	4.6x10 ⁵	4.4x10 ⁵
♀	2.3x10 ⁻⁵	0.123 (12) 0.119-0.127	8.0x10 ⁻⁴ (8) 7.7x10 ⁻⁴ -8.3x10 ⁻⁴	4.4x10 ⁵	4.2x10 ⁵
♂	2.1x10 ⁻⁵	0.100 (10) 0.098-0.108	7.0x10 ⁻⁴ (5) 6.8x10 ⁻⁴ -7.3x10 ⁻⁴	5.6x10 ⁵	5.4x10 ⁵
<i>A. aegypti</i>					
♀	6.0x10 ⁻⁶	0.182 (20) 0.200-0.173	1.1x10 ⁻³ (10) 9.9x10 ⁻⁴ -1.4x10 ⁻³	4.6x10 ⁴	3.0x10 ⁴

TABLE 2 (cont.)

Species & stage	Qt cm ³ /sec	l* = length cm	r* = mean radius cm	▲ P dyne /cm ²	▲ P*** cor- rected dyne/cm ²
<i>P. humanus</i>					
First	2.1x10 ⁻⁷	0.027 (10) 0.024-0.031	2.8x10 ⁻⁴ (5) 2.5x10 ⁻⁴ -3.2x10 ⁻⁴	6.1x10 ⁴	4.5x10 ⁴
Second	1.7x10 ⁻⁷	0.033 (12) 0.032-0.034	3.1x10 ⁻⁴ (6) 3.0x10 ⁻⁴ -3.4x10 ⁻⁴	3.9x10 ⁴	2.3x10 ⁴
♀	1.4x10 ⁻⁶	0.040 (10) 0.038-0.043	3.6x10 ⁻⁴ (5) 3.4x10 ⁻⁴ -3.9x10 ⁻⁴	2.1x10 ⁵	1.9x10 ⁵
♂	1.1x10 ⁻⁶	0.040 (12) 0.037-0.042	3.7x10 ⁻⁴ (5) 3.3x10 ⁻⁴ -3.9x10 ⁻⁴	1.5x10 ⁵	1.3x10 ⁵
<i>R. prolixus</i>					
Fifth***	3.3x10 ⁻⁴	0.020	5.0x10 ⁻⁴	1.96x10 ⁶ 9.12x10 ⁶	

* Mean
(number of insects used)
Range

** ▲ P "corrected" = ▲ P - capillary
blood pressure.

*** Data from Bennet-Clark (1963,
p. 223).

The Muscular Tension and the Power Output of the Cibarial Dilators

In *C. lectularius* the mean tension required of the cibarial pump dilators decreases from the first to the second nymphal instar and then increases to a maximum in the adult (tables 3 and 4). The value for the cibarial pump dilators of the male was larger than for those of the female. In the female *A. aegypti* the muscular tension required per unit sectional area of the cibarial pump dilators is larger than in the first three nymphal instars and smaller than in the other instars of *C. lectularius*. In *P. humanus* the mean muscular tension of the cibarial pump dilators decreases from the first to the second nymphal instar and reaches a maximum in the adult with a higher value in the female than in the male.

From the data published by Bennet-Clark (1963) the mean muscular tension required per cm² sectional area of the cibarial pump dilators of the fifth nymphal instar of *R. prolixus* was calculated to be in the range between 1.2 to 5.7 kg/cm².

TABLE 3. The mean force and muscular tension of the cibarial pump dilators in *C. lectularius*, female *A. aegypti*, *P. humanus*, and *R. prolixus*.

Species	Area of diaphragm* cm ²	Mean** force dynes	Mean*** muscular tension dynes	Cross sectional* area of muscles cm ²	Muscular tension dyne/cm ²
<i>C. lectularius</i>					
First	8.6x10 ⁻⁵ (5)	12.0	24.0	4.2x10 ⁻⁴ (5)	5.7x10 ⁴
	7.6x10 ⁻⁵ -9.4x10 ⁻⁵			3.7x10 ⁻⁴ -4.8x10 ⁻⁴	
Second	1.0x10 ⁻⁴ (7)	11.0	22.0	5.1x10 ⁻⁴ (5)	4.3x10 ⁴
	9.6x10 ⁻⁵ -1.4x10 ⁻⁴			4.7x10 ⁻⁴ -5.6x10 ⁻⁴	
Third	1.6x10 ⁻⁴ (5)	22.4	44.8	8.2x10 ⁻⁴ (6)	5.5x10 ⁴
	1.0x10 ⁻⁴ -2.1x10 ⁻⁴			7.9x10 ⁻⁴ -8.4x10 ⁻⁴	
Fourth	2.5x10 ⁻⁴ (5)	77.5	155.0	1.2x10 ⁻³ (6)	1.3x10 ⁵
	2.2x10 ⁻⁴ -2.9x10 ⁻⁴			1.0x10 ⁻³ -1.5x10 ⁻³	
Fifth	3.2x10 ⁻⁴ (5)	140.8	281.6	1.3x10 ⁻³ (5)	2.2x10 ⁵
	2.9x10 ⁻⁴ -3.7x10 ⁻⁴			1.0x10 ⁻³ -1.8x10 ⁻³	
♀	5.7x10 ⁻⁴ (8)	239.4	478.8	2.1x10 ⁻³ (7)	2.3x10 ⁵
	4.9x10 ⁻⁴ -5.9x10 ⁻⁴			1.9x10 ⁻³ -2.5x10 ⁻³	
♂	4.1x10 ⁻⁴ (5)	221.4	442.8	1.5x10 ⁻³ (8)	2.9x10 ⁵
	3.8x10 ⁻⁴ -4.5x10 ⁻⁴			1.2x10 ⁻³ -1.9x10 ⁻³	
<i>A. aegypti</i>					
♀	1.9x10 ⁻⁴ (10)	5.7	11.4	1.8x10 ⁻⁴ (10)	6.3x10 ⁴
	1.4x10 ⁻⁴ -2.3x10 ⁻⁴			1.3x10 ⁻⁴ -2.3x10 ⁻⁴	
<i>P. humanus</i>					
First	2.4x10 ⁻⁵ (6)	1.1	2.2	6.8x10 ⁻⁵ (5)	3.2x10 ⁴
	1.9x10 ⁻⁵ -2.7x10 ⁻⁵			6.1x10 ⁻⁵ -7.6x10 ⁻⁵	

TABLE 3 (cont.).

Species	Area of the diaphragm cm ²	Mean** force dynes	Mean*** muscular tension dynes	Cross sectional* area of muscles cm ²	Muscular tension dyne/cm ²
Second	4.5x10 ⁻⁵ (5)	1.0	2.0	1.1x10 ⁻⁴ (5)	1.8x10 ⁴
	3.9x10 ⁻⁵ -5.2x10 ⁻⁵			9.4x10 ⁻⁵ -1.7x10 ⁻⁴	
♀	8.1x10 ⁻⁵ (8)	15.4	30.8	1.9x10 ⁻⁴ (8)	1.6x10 ⁵
	7.3x10 ⁻⁵ -9.2x10 ⁻⁵			1.4x10 ⁻⁴ -2.5x10 ⁻⁴	
♂	6.4x10 ⁻⁵ (8)	8.3	16.6	2.0x10 ⁻⁴ (8)	8.3x10 ⁴
	5.8x10 ⁻⁵ -7.4x10 ⁻⁵			1.3x10 ⁻⁴ -2.2x10 ⁻⁴	
<i>R. prolixus</i>					
Fifth	9.8x10 ⁻³ (2)	1.9x10 ⁴⁺	3.8x10 ⁴⁺	3.2x10 ⁻² (2)	1.2x10 ⁶⁺
	9.6x10 ⁻³ -1.0x10 ⁻²	8.9x10 ⁴	17.8x10 ⁴	2.8x10 ⁻² -3.5x10 ⁻²	5.6x10 ⁶
*	Average (number of measurements)				
	Range				
**	Mean force = ▲ P x area of the diaphragm				
***	Mean muscular tension during working stroke = mean force x 2				
+	The two values correspond to the two different values of ▲ P of Bennet-Clark (see table 2).				

The muscular tension of the cibarial pump dilators most probably reaches a peak value of twice the estimated mean in table 3. Wigglesworth (1965) reported the maximum load a muscle can raise per square centimeter of cross section in some species and he found that there is no great difference between insects and vertebrates as the value for man is 6-10 kg, for the frog 3 kg, for the mandibular muscles of insects 3.6-6.9 kg, for the hind leg of *Tettigonia* 4.7 kg and for the flexor tibia of *Decticus* 5.9 kg.

The power output of the cibarial pump dilators expressed as erg/sec/g of muscle and as g cm/sec/g of muscle are shown in table 4. In *C. lectularius* the power developed by these muscles, like the muscular tension, decreases from the first to the second nymphal instar and then increases to a maximum in the adult stage. In the female *A. aegypti* the power output/g of muscle was higher than that of the first three nymphal instars and lower than that of the fifth instar and the adult of *C. lectularius*.

TABLE 4. The power output of the cibarial pump dilators in *C. lectularius*, female *A. aegypti*, *P. humanus*, and *R. prolixus*.

Species & stage	Travel of* diaphragm cm	Pump cycles/second	Travel of diaphragm cm/sec	Power** output erg/sec	Length of* muscles cm	Weight of muscles g	Power output in erg/sec/g
<i>C. lectularius</i>							
First	2.4 x 10 ⁻³ (5)	4.0	9.6 x 10 ⁻³	0.12	0.015 (6)	6.3 x 10 ⁻⁶	1.9 x 10 ⁴
	2.1 x 10 ⁻³ - 2.7 x 10 ⁻³				0.012 - 0.017		
Second	2.6 x 10 ⁻³ (7)	3.8	9.9 x 10 ⁻³	0.11	0.017 (7)	8.7 x 10 ⁻⁶	1.3 x 10 ⁴
	2.4 x 10 ⁻³ - 2.8 x 10 ⁻³				0.013 - 0.019		
Third	3.6 x 10 ⁻³ (5)	3.3	4.2 x 10 ⁻²	0.27	0.022 (5)	1.8 x 10 ⁻⁵	1.5 x 10 ⁴
	3.2 x 10 ⁻³ - 3.9 x 10 ⁻³				0.019 - 0.025		
Fourth	4.5 x 10 ⁻³ (5)	3.3	4.5 x 10 ⁻²	4.20	0.026 (5)	3.1 x 10 ⁻⁵	3.9 x 10 ⁴
	4.1 x 10 ⁻³ - 4.9 x 10 ⁻³				0.021 - 0.031		
Fifth	6.2 x 10 ⁻³ (5)	3.0	4.9 x 10 ⁻²	2.70	0.028 (8)	3.6 x 10 ⁻⁵	7.5 x 10 ⁴
	5.8 x 10 ⁻³ - 6.6 x 10 ⁻³				0.025 - 0.034		
♀	7.5 x 10 ⁻³ (8)	2.4	4.8 x 10 ⁻²	4.30	0.033 (8)	6.9 x 10 ⁻⁵	6.2 x 10 ⁴
	6.8 x 10 ⁻³ - 7.9 x 10 ⁻³				0.029 - 0.037		

♂	7.5 x 10 ⁻³ (5)	2.4	1.8 x 10 ⁻²	3.99	0.030 (5)	4.5 x 10 ⁻⁵	8.9 x 10 ⁴
	6.8 x 10 ⁻³ - 7.8 x 10 ⁻³				0.027 - 0.034		
<i>A. aegypti</i>							
♀	3.3 x 10 ⁻³ (10)	4.9	1.6 x 10 ⁻²	0.09	0.013 (10)	2.3 x 10 ⁻⁶	3.9 x 10 ⁴
	2.9 x 10 ⁻³ - 3.7 x 10 ⁻³				0.010 - 0.015		
<i>P. humanus</i>							
First	1.0 x 10 ⁻³ - 3.9 x 10 ⁻³ (6)	2.8	3.0 x 10 ⁻³	0.003	3.5 x 10 ⁻³ (6)	2.4 x 10 ⁻⁷	1.3 x 10 ⁴
	9.5 x 10 ⁻⁴ - 1.4 x 10 ⁻³				3.0 x 10 ⁻³ - 3.9 x 10 ⁻³		
Second	1.5 x 10 ⁻³ (5)	5.3	8.0 x 10 ⁻³	0.008	5.2 x 10 ⁻³ (5)	5.7 x 10 ⁻⁷	1.4 x 10 ⁴
	1.3 x 10 ⁻³ - 1.7 x 10 ⁻³				4.9 x 10 ⁻³ - 5.5 x 10 ⁻³		
♀	3.0 x 10 ⁻³ (7)	4.6	1.4 x 10 ⁻²	0.216	9.2 x 10 ⁻³ (7)	1.7 x 10 ⁻⁶	1.3 x 10 ⁵
	2.7 x 10 ⁻³ - 3.4 x 10 ⁻³				8.8 x 10 ⁻³ - 9.5 x 10 ⁻³		
♂	3.0 x 10 ⁻³ (6)	4.2	1.3 x 10 ⁻²	0.108	8.7 x 10 ⁻³ (6)	1.7 x 10 ⁻⁶	6.3 x 10 ⁴
	2.5 x 10 ⁻³ - 3.4 x 10 ⁻³				8.3 x 10 ⁻³ - 9.0 x 10 ⁻³		
<i>R. prolixus</i>							
Fifth	0.016	3.0	0.048	912	0.05	1.6 x 10 ⁻³	5.7 x 10 ⁵
				4.3 x 10 ³			2.7 x 10 ⁶

* Average (number of insects)
Range

** Power output = mean force x travel of the diaphragm in a second.

TABLE 4. The power output of the cibarial pump dilators in *C. lectularius*, female *A. aegypti*, *P. humanus*, and *R. prolixus*.

Species & stage	Travel of* diaphragm cm	Pump cycles/second	Travel of diaphragm cm/sec	Power** erg/sec	Length of* muscles cm	Weight of muscles g	Power output in erg/sec/g
<i>C. lectularius</i>							
First	2.4 x 10 ⁻³ (5) 2.1 x 10 ⁻³ - 2.7 x 10 ⁻³	4.0	9.6 x 10 ⁻³	0.12	0.015 (6) 0.012 - 0.017	6.3 x 10 ⁻⁶	1.9 x 10 ⁴
Second	2.6 x 10 ⁻³ (7) 2.4 x 10 ⁻³ - 2.8 x 10 ⁻³	3.8	9.9 x 10 ⁻³	0.11	0.017 (7) 0.013 - 0.019	8.7 x 10 ⁻⁶	1.3 x 10 ⁴
Third	3.6 x 10 ⁻³ (5) 3.2 x 10 ⁻³ - 3.9 x 10 ⁻³	3.3	1.2 x 10 ⁻²	0.27	0.022 (5) 0.019 - 0.025	1.8 x 10 ⁻⁵	1.5 x 10 ⁴
Fourth	4.5 x 10 ⁻³ (5) 4.1 x 10 ⁻³ - 4.9 x 10 ⁻³	3.3	1.5 x 10 ⁻²	1.20	0.026 (5) 0.021 - 0.031	3.1 x 10 ⁻⁵	3.9 x 10 ⁴
Fifth	6.2 x 10 ⁻³ (5) 5.8 x 10 ⁻³ - 6.6 x 10 ⁻³	3.0	1.9 x 10 ⁻²	2.70	0.028 (8) 0.025 - 0.034	3.6 x 10 ⁻⁵	7.5 x 10 ⁴
♀	7.5 x 10 ⁻³ (8) 6.8 x 10 ⁻³ - 7.9 x 10 ⁻³	2.4	1.8 x 10 ⁻²	4.30	0.033 (8) 0.029 - 0.037	6.9 x 10 ⁻⁵	6.2 x 10 ⁴
♂	7.5 x 10 ⁻³ (5) 6.8 x 10 ⁻³ - 7.8 x 10 ⁻³	2.4	1.8 x 10 ⁻²	3.99	0.030 (5) 0.027 - 0.034	4.5 x 10 ⁻⁵	8.9 x 10 ⁴
<i>A. aegypti</i>							
♀	3.3 x 10 ⁻³ (10) 2.9 x 10 ⁻³ - 3.7 x 10 ⁻³	4.9	1.6 x 10 ⁻²	0.09	0.013 (10) 0.010 - 0.015	2.3 x 10 ⁻⁶	3.9 x 10 ⁴
<i>P. humanus</i>							
First	1.0 x 10 ⁻³ - 3.9 x 10 ⁻³ (6) 9.5 x 10 ⁻⁴ - 1.4 x 10 ⁻³	2.8	3.0 x 10 ⁻³	0.003	3.5 x 10 ⁻³ (6) 3.0 x 10 ⁻³ - 3.9 x 10 ⁻³	2.4 x 10 ⁻⁷	1.3 x 10 ⁴
Second	1.5 x 10 ⁻³ (5) 1.3 x 10 ⁻³ - 1.7 x 10 ⁻³	5.3	8.0 x 10 ⁻³	0.008	5.2 x 10 ⁻³ (5) 4.9 x 10 ⁻³ - 5.5 x 10 ⁻³	5.7 x 10 ⁻⁷	1.4 x 10 ⁴
♀	3.0 x 10 ⁻³ (7) 2.7 x 10 ⁻³ - 3.4 x 10 ⁻³	4.6	1.4 x 10 ⁻²	0.216	9.2 x 10 ⁻³ (7) 8.8 x 10 ⁻³ - 9.5 x 10 ⁻³	1.7 x 10 ⁻⁶	1.3 x 10 ⁵
♂	3.0 x 10 ⁻³ (6) 2.5 x 10 ⁻³ - 3.4 x 10 ⁻³	4.2	1.3 x 10 ⁻²	0.108	8.7 x 10 ⁻³ (6) 8.3 x 10 ⁻³ - 9.0 x 10 ⁻³	1.7 x 10 ⁻⁶	6.3 x 10 ⁴
<i>R. prolixus</i>							
Fifth	0.016	3.0	0.048	912 4.3 x 10 ³	0.05	1.6 x 10 ⁻³	5.7 x 10 ⁵ 2.7 x 10 ⁶

* Average (number of insects) Range

** Power output = mean force x travel of the diaphragm in a second.

It is also higher than that of the first two instars and lower than that of the adult *P. humanus*.

Roeder (1953) reported the power of the flight muscles in some insects. The minimum was 205 g cm/sec/g of muscle for *Vanessa atalanta* L. and the maximum was 558 g cm/sec/g of muscle for *Aeschna mixta* Latr. The cibarial pump dilators in *C. lectularius*, *A. aegypti*, and *P. humanus* are not required to operate at specific power outputs as great as these. The dilators of the cibarial pump of the fifth nymphal instar of *R. prolixus*, on the other hand, would, on the basis of Bennet-Clark's data, be required to work at a greater specific power output than the flight muscles of these insects.

Discussion

The actual laws of blood flow, at least in the range of physiological rates of flow, approximate sufficiently the simple laws (e.g. Poiseuille's law) for these to be applied with caution, using the appropriate value for the effective viscosity rather than the value obtained in viscometers of a large bore. Burton (1965) stated "As long as the diameter of the capillary tube used in the viscometer is more than 1 or 2 mm, the relative viscosity of the blood is the same, whatever the size of the tube used. When, however, tubes of narrower diameter are used, the value for relative viscosity found is less. This is because the absolute viscosity of water is the same however small the diameter of the tube; but that of the blood decreased to less than half the value found when large tubes are used". This has long been known as the Fahraeus-Lindquist effect. From this the viscosity value and consequently the values of ΔP obtained in my calculations could be in error by a factor of 2. Burton (1965) also discusses the effect of temperature on viscosity of the blood. I should not expect significant variation in the viscosity of the blood through changes in temperature in the quick pumping process of sucking in these insects.

The ability to feed at a relatively high rate through a minute feeding canal is very important for blood-sucking insects. For this purpose they are equipped with very efficient feeding apparatus with a sucking pump which is capable of exerting a high tension on the blood upon which they feed. Differences in the rate of feeding in the different blood-sucking insects can be due to many factors. One of these factors is the negative pressure that can be produced in the cibarial pump. This in turn is dependent upon the tension which can be developed in the cibarial pump dilators, the length of the feeding canal and its diameter as well as the viscosity of the blood and the capillary blood pressure of the host. These experiments suggest that blood viscosity and the capillary blood pressure of the host might be of importance in the evolution of host selection in blood-sucking insects.

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